

THE ASTERACEAE OF THE GUIANAS, III:  
VERNONIEAE AND RESTORATION OF THE  
GENUS *XIPHCHAETA*

HAROLD ROBINSON

ABSTRACT

The tribe Vernonieae is surveyed in continuation of the preliminary reviews of the Asteraceae of the Guianas (Guyana, Suriname, Cayenne), South America. Nineteen species are listed in 15 genera. The genus *Xiphochaeta* is resurrected from the synonymy of *Stilpnopappus* for the northern South American species commonly known as *S. viridis*. Elongate raphids in the achene are emphasized as a character relating *Xiphochaeta* to *Lepidaploa*.

Key Words: Asteraceae, Vernonieae, pollen, *Xiphochaeta*, Guianas, South America

The Flora of the Guianas project has been generally described by Funk (1991) in the first of a series of preliminary reviews of the family Asteraceae in that area. Her 1991 paper treated the tribe Heliantheae while a second study is projected for tribes Anthemideae, Astereae, Lactuceae, Cynareae, Mutisieae, and Senecioneae. The original intent was to treat the Eupatorieae and Vernonieae together in a third paper, but special needs of the Vernonieae have led to a decision to treat that tribe here, separately.

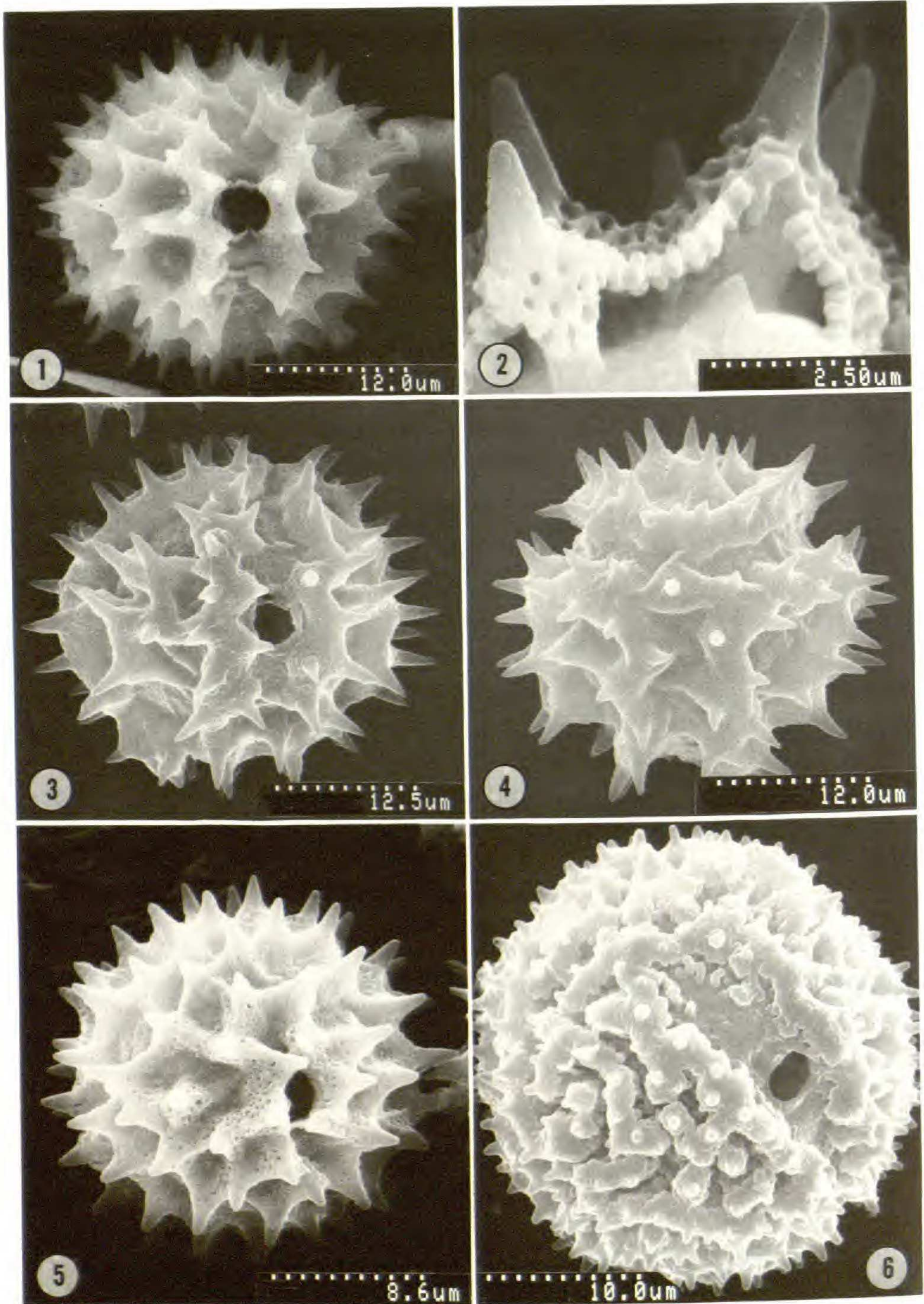
A key to the genera and a list of the species of the Vernonieae is provided as in other preliminary studies. However, the present study is the first to use many recent generic segregates of the Vernonieae in a floristic work. These recent generic segregates, plus a genus resurrected here from synonymy, and previously accepted genera are all keyed in greater detail than usual. Features of the pollen are particularly useful in the Vernonieae, and details of pollen structure are included in the key.

I have dealt with many segregates of traditional *Vernonia* Schreb. in a number of papers. Four of these papers, those dealing with *Cyrtocymura* H. Robinson (Robinson, 1987), *Lepidaploa* (Cass.) Cass. (Robinson, 1990b), *Vernonanthura* H. Robinson (Robinson, 1992), and the introduced paleotropical *Cyanthillium* Blume (Robinson, 1990a), include species in the Guianas. An additional genus, *Xiphochaeta* Poeppig in Poeppig and Endlicher, is restored here for the single species *X. aquatica* Poeppig that is commonly

known as *Stilpnopappus viridis* Benth. ex Baker, occurring in the Guianas and in the Orinoco and northern Amazon basins. The sample of Vernonian neotropical genera occurring in the area is limited, but an initial attempt to use the segregates and the pollen types in a flora is considered important.

Pollens are particularly interesting in the Vernonieae. Pollen variations are numerous and striking (Stix, 1960; Kingham, 1976; Keeley and Jones, 1977) and some of the variations were noticed and used taxonomically as early as the work of Steetz in 1864. The work of Steetz was cited by Bentham and Hooker (1873), but use of pollen as a taxonomic character in the Vernonieae was allowed to lapse almost completely for over a hundred years. This lapse in use of pollen as a character coincided with the period of entrenchment of an excessively broad concept of the genus *Vernonia*. More recently, pollen is one of a series of characters such as style bases and anther appendages, observable with the compound microscope, that prove useful in delimiting natural groups in the Vernonieae. The point has been reached where I believe every taxonomic treatment in the Vernonieae should include mention of pollen type (Robinson, 1988). To aid in use of pollen, SEM illustrations are provided, but almost all the taxonomically important features, such as patterns of muri, colpi, spines and completeness of tectum, can be observed easily with the compound microscope.

General terminology used for various pollen types in the Vernonieae dates initially from Keeley and Jones (1977) and Jones (1981), with elaborations by Robinson (1988, 1990b). Type A is tricolporate and spinose with a perforated tectum continuous over all non-colpar areas (Figure 2). In spite of some variations within the Type A, no formal subdivisions have been established, and only some of the genera with Type A pollen are shown here (*Centratherum*, *Cyrtocymura*, and *Trichospira*; Figures 1–5). A modified Type A in *Orthopappus* has numerous irregularly crowded muri with narrow areas of discontinuous perforated tectum between (Figure 6). Type B, which is not found in the Guianas, is tricolporate and lophate with distinct areoles, the perforated tectum is restricted to the muri, there are three equatorial areoles between the colpi, and the muri are attached to the footlayer by large baculae. Type C, seen in the Guianas in *Lepidaploa*, is tricolporate and lophate with tectum restricted to the muri; there are two equatorial areoles between the colpi, there is a polar areole,

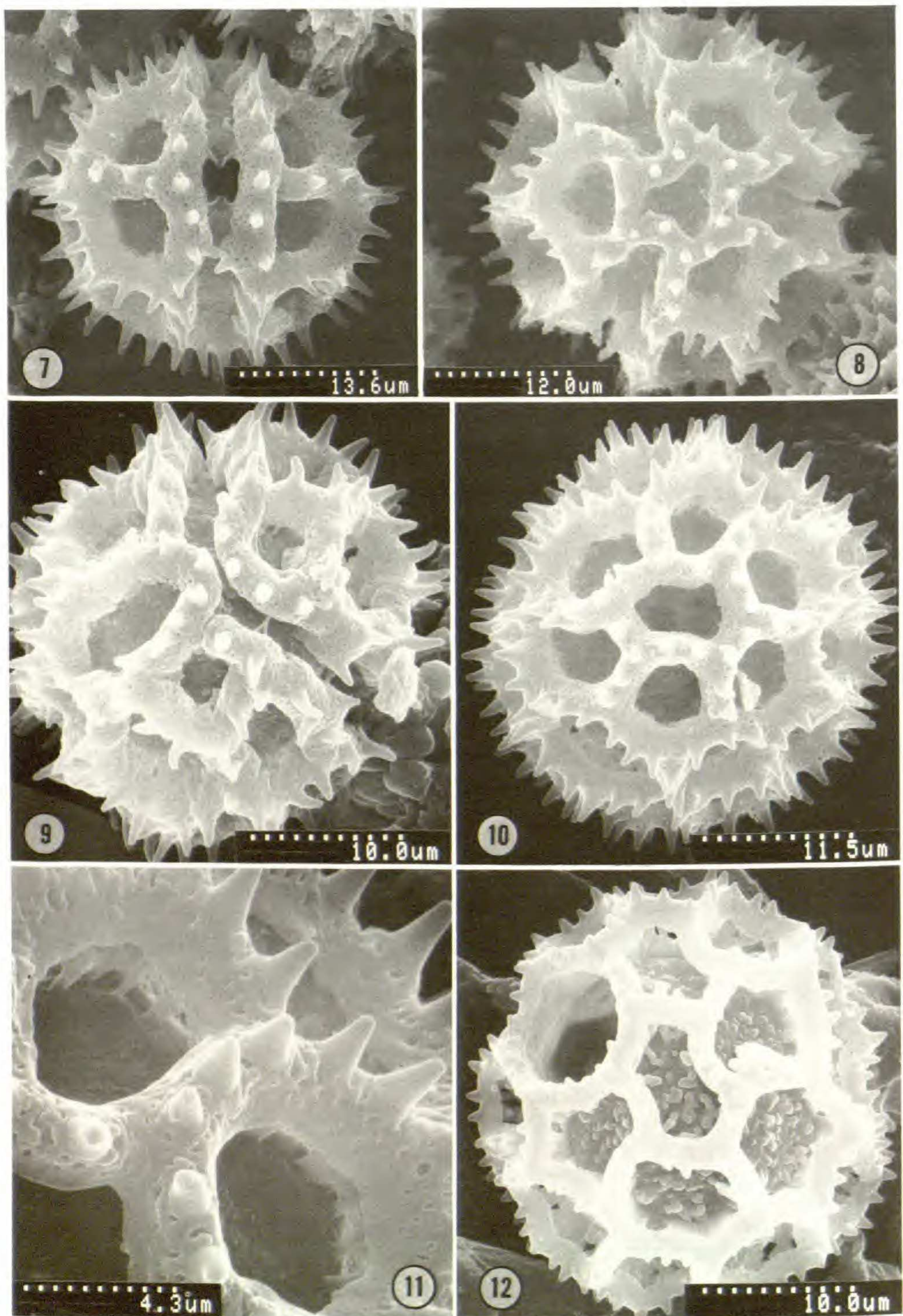


Figures 1–6. Pollens of Guiana Vernoniae, tricolporate, Type A. 1, 2. *Centratherum punctatum* Cass., Brazil, *Irwin 27191* (US): 1. colpate view showing pore, 2. broken grain showing continuous perforated tectum between spines. 3, 4. *Cytocymura scorpioides* (Lam.) H. Robinson, Brazil, *Beetle 2029* (US): 3. colpate view, 4. polar view. 5. *Trichospira verticillata* (L.) Blake, Venezuela, *Velez 2638* (US), equatorial view showing colpus and part of intercolpus. 6. *Orthopappus angustifolius* (Sw.) Gleason, Bolivia, *Buchtien 785* (US), oblique view showing colpus and part of intercolpus.

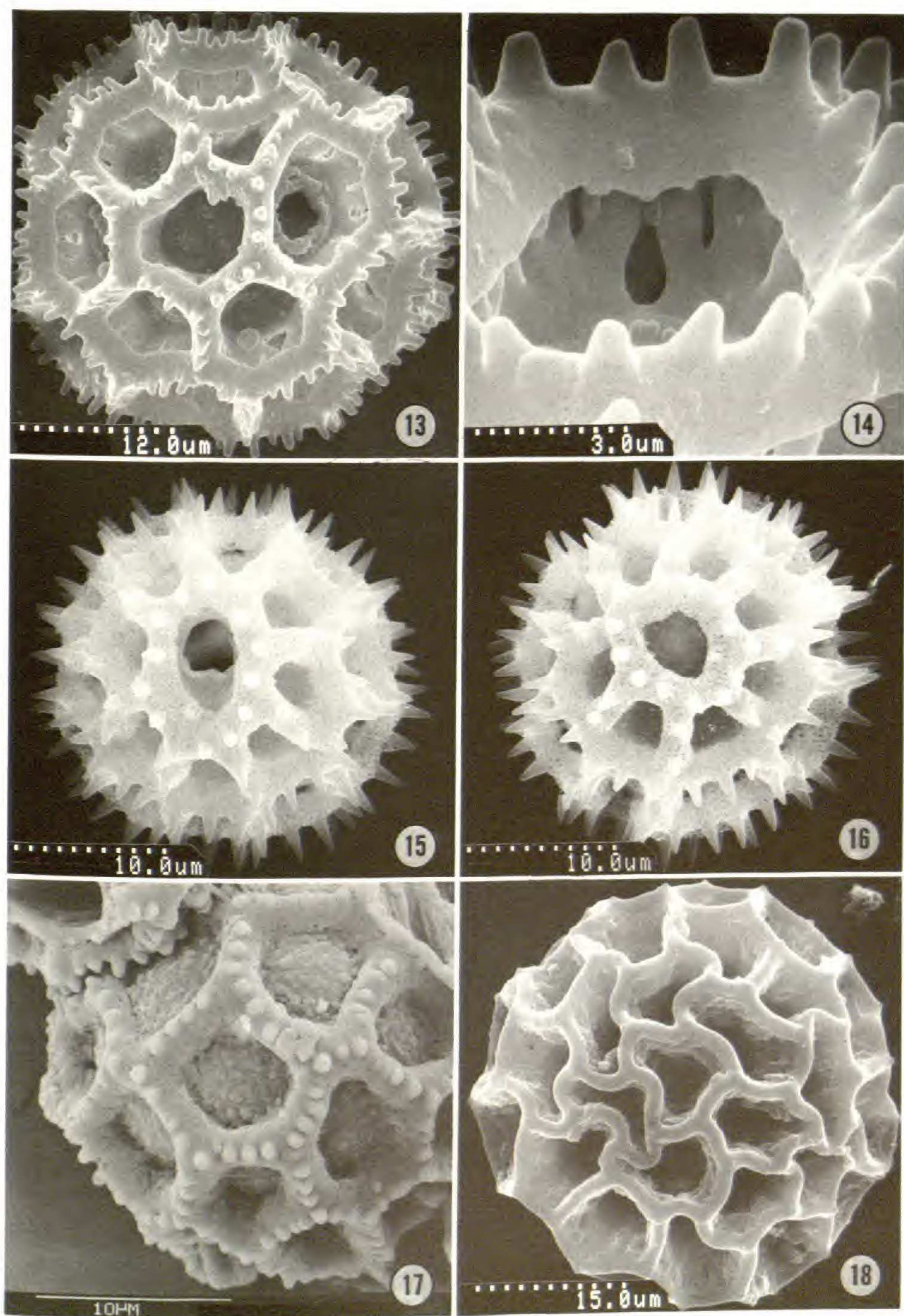
and the muri are weakly attached to the footlayer (Figures 7 and 8). Type D, which is not presently known from the Guianas, is tricolporate and lophate like Type C but without a polar areole and with cross-walls in the colpi above and below the pores. Type E, found in the Guianas in *Pacourina*, is triporate and has the complete surface covered with areoles of similar size including three that contain the pores; the muri have smooth crests without a perforated tectum, and the crests are firmly attached to the footlayer by an irregular bacular structure (Figure 18). Type F, found in *Elephantopus*, *Pseudelephantopus* and *Rolandra*, is triporate and multiareolate as in Type E, but usually has a perforated tectum on the muri and has many short spinules borne along the crests of the muri (Figures 10–14). Type G, found commonly in *Lepidaploa* but seen in the Guianas in *Xiphochaeta*, is tricolporate like Types C and D without the polar areoles or the divided colpi (Figure 9). Type H is added here for the pollen of the introduced *Cyanthillium*, which is areolate over the whole surface as in E and F, but has a perforated tectum on the muri, and lacks strong baculae between the intersections of the muri (Figures 15–16). Type J is added here for the unusual pollen of *Sparganophorus* that is lophate over the whole surface, triporate with short points as in F, but has low, almost sessile muri and has a weak perforated tectum continuous across the areoles (Figure 17). The low muri of *Sparganophorus* are obvious under the compound microscope, where they appear vestigial.

Some of the diversity of pollen in the tribe is evident in the accompanying SEM photographs for most of the genera and all the basic pollen types in the Guianas. The pollen sizes cited in the key and text are in fluid. Measurements include the tectum but exclude the projecting spine tips. Grains appear under SEM at about  $\frac{2}{3}$  of the size in fluid.

The study of the pollen suggests certain comparative relationships in the Vernoniae of the area. Among those genera included in broader traditional concepts of *Elephantopus*, both the pollen and the pappus indicate *Orthopappus* is much more distinct than *Pseudelephantopus*. *Orthopappus* should be maintained as distinct from *Elephantopus* even when *Pseudelephantopus* is reduced to synonymy. *Rolandra* and the closely related *Spiracantha* of Central and northern South America have the same type of lophate grains, often lacking perforations in the tectum on the muri. The generally annual nature, the distinctive foliose bracts under the



Figures 7–12. Pollens of Guiana Vernoniaeae, lophate forms. 7–9. Tricolporate forms. 7, 8. *Lepidaploa cotoneaster* (Less.) H. Robinson, Brazil, *Hatschbach 45153* (us), Type C: 7. colpar view, 8. polar view. 9. *Xiphochaeta aquatica* Poeppig in Poeppig & Endlicher, Peru, *Rimachi 4672* (us), Type G, polar view. 10–12. Triporate forms, Type F. 10, 11. *Elephantopus mollis* H.B.K., Rota, Marianas Isl., *Fosberg 31849* (us), Type F: 10. polar view, 11. Detail of muri showing baculae attached to footlayer. 12. *Pseudelephantopus spicatus* (Juss. ex Aubl.) Rohr, Cuba, *Morton 4048* (us), Type F, view showing pore.



Figures 13–18. Pollens of Guiana Vernoniae, lophate, triporate forms. 13, 14. *Rolandra fruticosa* (L.) O. Kuntze, Brazil, *MacLeish 760* (us), Type F: 13, view showing pore, 14, detail of muri showing baculae attached to footlayer, variant that lacks perforations in tectum. 15, 16. *Cyanthillium cinerea* (L.) H. Robinson, Cayenne, *Broadway 442* (us), Type H, muri near margins showing lack of baculae between junctures: 15, view showing pore, 16, polar view. 17. *Sparganophorus sparganophora* (L.) Jeffrey, Venezuela, *Liesner 13370* (us), Type J, view showing low muri and showing part of adjacent broken grain. 18. *Pacourina edulis* Aubl., Colombia, *Killip & Smith 14576* (us), Type E, view showing smooth crests of muri and irregular bacular structure.

heads of the latter, and the pappus of long scales rather than a dentate crown are the basis for its continued separate generic status.

Chromosome numbers obtained from the summary by Jones (1979) are given below in the key to the genera of the Guianas. The genera with tricolporate pollen in the Guianas show chromosome numbers mostly based on  $n = 17$ . The genera with triporate pollen have base numbers, where known, of  $n = 8$ ,  $n = 9$ ,  $n = 10$ ,  $n = 11$ , or  $n = 13$ . Tricolporate Vernonieae with chromosome numbers near  $n = 10$  are not presently known from the Guianas, and are known in the Neotropical Region only in the occasionally introduced *Baccharoides anthelminthica* (L.) Moench and *Ethulia conyzoides* L.f.

Most of the 19 species of the Vernonieae occurring in the Guianas also occur in adjacent regions such as Venezuela and Brazil. Some such as *Cyrtocymura scorpioides* occur through much of tropical America. One species, *Lepidaploa chrysotricha*, is endemic to Guyana.

ARTIFICIAL KEY TO THE GENERA OF  
THE VERNONIEAE IN THE GUIANAS

1. Individual heads with 1–5 (–6) florets, sometimes compacted in units of many heads . . . . . 2
2. Individual heads discrete, with many easily deciduous inner involucre bracts; pappus in 2 series; pollen Type A (as in Figures 1, 2);  $n = 17$  where known . . . . . 3
3. Pappus of many bristles; anther thecae with basal tails formed with distinct sharp points of thick-walled, sterile cells; style base with broadened node and basal ring of sclerified cells;  $n = 17$  . . . . . *Piptocarpha*
3. Pappus of few flattened ribbons or short scales; anther thecae without sharp basal tails of thick-walled cells, bases blunt or with thin-walled cells; style base without node or sclerified cells . . . . . *Pollalesta*
2. Heads compacted into secondary clusters, often grouped in axils of specialized bracts; pappus of only 1 series;  $n = 8?$ ,  $n = 11$ ,  $n = 13$  where known . . . . . 4
4. Shrubs; clusters of heads in axils of scarcely reduced leaves, each head with 1 floret; pappus an irregularly dentate crown; achene without setulae, densely cov-

- ered with glands; anther collar shorter than basal spurs of anther thecae; pollen Type F (Figures 13, 14), with or without perforations in tectum on muri, ca. 40  $\mu\text{m}$  in diam.;  $n = 8?$  (in closely related *Spiracantha*) . . . . . *Rolandra*
4. Herbs; clusters of heads borne well above larger basal leaves, each head with usually 5 florets; pappus of bristles or awns; achene with many setulae; anther collar longer than basal spurs of anther thecae; pollen Types A or F . . . . . 5
5. Pappus of many bristles; pollen a modified Type A (Figure 6), 35–40  $\mu\text{m}$  in diam.;  $n = 11$  . . . . . *Orthopappus*
5. Pappus of 5 awns; pollen Type F, lophate without distinct colpi (Figures 10–12), ca. 40  $\mu\text{m}$  in diam. . . . . 6
6. Pappus awns highly contorted or sinuous;  $n = 13$  . . . . . *Pseudelephantopus*
6. Pappus awns straight;  $n = 11$  . . . . . *Elephantopus*
1. Individual heads with 10 or more florets, not compacted into distinct secondary clusters . . . . . 7
7. Inflorescence with heads in axils of subopposite leaves; florets of heads intermixed with narrow pales; achenes compressed, with 2 awns; pollen Type A (Figure 5), 25–30  $\mu\text{m}$  in diam. . . . . *Trichospira*
7. Inflorescence with leaves or bracts alternate like the vegetative leaves; heads without pales; achenes terete or prismatic . . . . . 8
8. Pappus consisting of an expanded sclerified or carnose collar, without bristles or awns; pollen Type J (Figure 17), lophate with low muri, polyhedral without colpi, weak perforated tectum in areoles, 25–35  $\mu\text{m}$  in diam. . . . . *Sparganophorus*
8. Pappus without expanded sclerified or carnose collar, with bristles or awns . . . . . 9
9. Pappus of many short easily deciduous segments, less than  $\frac{1}{3}$  as long as the corolla . . . . . 10
10. Heads in axils of large leaves; plants semi-aquatic; leaves with weakly spinose margins; pollen Type E (Figure 18), ca. 65  $\mu\text{m}$  in diam. . . . . *Pacourina*



10. Heads terminal, with subtending series of narrow foliose bracts below involucre; plants not semi-aquatic; pollen Type A (Figures 1, 2), 40–50  $\mu\text{m}$  in diam.;  $n = 16$  . . . *Centratherum*
9. Pappus of many bristles  $\frac{2}{3}$  as long as corolla or longer, persistent to moderately deciduous . . . . . 11
11. Heads never sessile; without large bracts or leaves in inflorescence; stems pilosulous with T-shaped hairs; pollen Type H (Figures 15, 16), lophate, non-colpate, ca. 40  $\mu\text{m}$  in diam.;  $n = 9, 10, 18$  . . . . . *Cyanthillium*
11. Heads often sessile or appearing sessile due to lateral innovation; stems with or without T-shaped hairs; pollen colpate;  $n = 17$  where known . . . . . 12
12. Pollen Type A; heads not borne in axils of obvious foliose bracts; raphids of achene wall short or elongate . . . . . 13
13. Heads densely borne on scorpioid cymes, often contiguous; tips of involucre bracts usually pubescent on both surfaces; corolla lobes with hairs, without obvious internal resin ducts in center of lobe; raphids of achene walls elongate; pollen ca. 40  $\mu\text{m}$  in diam. (Figures 3, 4);  $n = 17$  . . . . .  
 . . . . . *Cyrtocymura*
13. Heads separated in cymose but not scorpioid inflorescences; tips of involucre bracts not pubescent inside; corolla lobes without hairs, often with longitudinal resin ducts filling center of lobe; raphids of achene walls subquadrate to short-oblong; pollen ca. 40  $\mu\text{m}$  in diam.  $n = 17$  . . . . .  
 . . . . . *Vernonanthura*
12. Pollen Types C and G; heads usually borne in axils of small or large foliose bracts; raphids of achene wall elongate . . . . . 14
14. Pappus of greatly thickened somewhat deciduous subulate bristles; plants

subaquatic; achene without distinct carpopodium; anther spurs shorter than anther collar; anther appendages small, bearing glands; corolla lobes with only glands; pollen Type G (Figure 9), 37–40  $\mu\text{m}$  in diam. . .

..... *Xiphochaeta*

14. Pappus of slender bristles, usually with distinct outer series of persistent scales; plants terrestrial, sometimes riverine; achene with large carpopodium; spurs of anther longer than anther collar; anther appendages usually without glands; corolla lobes usually with hairs or spicules; pollen Types C (Figures 7, 8), D, G, 45–50 (–60)  $\mu\text{m}$  in diam.;  $n = 17$  .....

..... *Lepidaploa*

### Genus and Species List

#### COMPOSITAE: TRIBE VERNONIEAE

##### **Centratherum** Cass.

*C. punctatum* Cass.

##### **Cyanthillium** Blume

*C. cinereum* (L.) H. Robinson

[Introduced, naturalized, originally paleotropical.]

##### **Cyrtocymura** H. Robinson

*C. scorpioides* (Lam.) H. Robinson

##### **Elephantopus** L.

*E. mollis* H.B.K.

##### **Lepidaploa** (Cass.) Cass.

*L. bolivarensis* (Badillo) H. Robinson

(syn. *Vernonia glandulosa* Badillo, 1946, not *V. glandulosa* DC., 1836).

*L. chrysotricha* (Alexander) H. Robinson

*L. ehretifolia* (Benth.) H. Robinson

*V. schomburgkiana* Schultz Bip.

*L. gracilis* (H.B.K.) H. Robinson

*V. moritziana* Schultz Bip.

*L. remotiflora* (L. C. Rich.) H. Robinson

##### **Orthopappus** Gleason

*O. angustifolius* (Swartz) Gleason

**Pacourina** Aubl.*P. edulis* Aubl.**Piptocarpha** R. Brown*P. triflora* (Aubl.) Benn. ex Baker**Pollalesta** H.B.K.*P. schomburgkii* (Schultz Bip.) Aristeg.**Pseudelephantopus** Rohr*P. spicatus* Rohr**Rolandra** Rottb.*R. fruticosa* (L.) O. Kuntze**Sparganophorus** Boehm. in Ludwig.*Sparganophorus sparganophora* (L.) C. Jeffrey(syn. *Sparganophorus vaillantii* Cranz, *Struchium sparganophora* (L.) O. Kuntze).

[For discussion of the use of these names see Jeffrey (1988).]

**Trichospira** H.B.K.*T. verticillata* (L.) Blake(syn. *Bidens verticillata* L., *Trichospira menthoides* H.B.K.).**Vernonanthura** H. Robinson*V. brasiliana* (L.) H. Robinson**Xiphochaeta** Poeppig in Poeppig & EndlicherPoeppig in Poeppig & Endlicher, *Nova. Gen. Sp.* 3: 44. 8–11. 1843.

The genus *Xiphochaeta* is here resurrected from the synonymy of *Stilpnopappus*. The following detailed description is provided to allow proper comparison with related genera.

Plants herbaceous, aquatic or semi-aquatic annuals or short-lived perennials, suberect from decumbent bases, moderately branched; stems with appressed antrorse puberulence. Leaves alternate, sessile or shortly petiolate; blades oblong to lanceolate, 2–5 cm long, 1–2 cm wide, base and apex acute, margins entire or minutely and remotely denticulate, upper surface appressed-puberulous, below glandular-punctate and minutely sparsely sericeous, venation ascending-pinnate. Heads in axils of leaves, sessile, solitary or rarely paired or ternate, homogamous; involucre bracts 70–80, graduated, unequal, 3–4-seriate, papery, 2–4 mm long, ca. 1 mm wide, green, margins ciliate above, outside slightly pilose and glanduliferous, apex shortly aristate, spreading with age; receptacle glabrous, non-paleaceous. Florets ca. 30 in a head; corollas regular, to 3 mm long, mostly glabrous; basal tube slender, elongate; throat short, lobes bearing glands at tip; anther collar elongate, with no subquadrate cells; anther thecae small, with basal spurs shorter than the collar; style base with node; style

branches glanduliferous outside. Achenes narrowly oblong or narrowed to base, to 2 mm long, base with numerous glands, with short setulae having paired cells very unequal, rarely uniseriate, resinous idioblasts sparse, usually solitary, raphids elongate; carpodium undifferentiated; pappus setae irregularly biseriate, rigidly subulate, incrassate, moderately deciduous, convex outside, concave inside, non-costate; outer setae ca. 15, 1.0–1.2 mm long; interior setae ca. 10, to 2.2 mm long, with ciliate margins. Pollen grains Type G, 37–40  $\mu\text{m}$  in diameter (Figure 9).

The species on which the genus is based has been recognized by all authors as not being *Vernonia* because of the unusual incrassate pappus segments. These details of the pappus, along with pollen and other characters, have now shown that the species is also out of place in *Stilpnopappus*, where it was placed by Baker (1873) and other more recent authors. The name *Xiphochaeta* appropriately reflects the distinctive sword-like elements of the pappus.

The genus resembles in habit the widespread *Sparganophorus* Boehm. of both hemispheres. The latter genus has a different kind of distinctive pappus that is a sclerified collar without bristles, and the pollen is lophate of a unique form (Figure 17). Structure and geography indicate that the relationship of *Xiphochaeta* to *Sparganophorus* is rather remote.

The broadened subulate pappus segments of *Xiphochaeta* were the basis of inclusion of the species in *Stilpnopappus* Mart. ex DC. The latter genus occurs mostly in eastern Brazil with two species in Venezuela, and it has broadened, flat pappus segments with a central costa and lateral wings. *Xiphochaeta* differs clearly by the heads being in the axils of full-sized leaves, by the presence of thicker, externally convex, non-costate segments of the pappus, and by the thin-walled glanduliferous anther appendages. The anther appendages in *Stilpnopappus* are much larger, without glands, and with ornate thickenings on the cell walls, particularly in a median stripe. Pollen grains of *Stilpnopappus* are Types D and G, and are ca. 50–55  $\mu\text{m}$  in diameter, much larger than in *Xiphochaeta*. The anther thecae of *Stilpnopappus* have well-developed, broad-based, and sometimes partially sterile spurs, unlike *Xiphochaeta*. The anther bases and appendages, more than any other characters, seem to negate any close relationship between *Xiphochaeta* and *Stilpnopappus*.

The closest relationship of *Xiphochaeta* is evidently to the common neotropical genus *Lepidaploa*. The habit of axillary heads,

shape of the involucre, and Type G pollen are all common in the latter genus. Pollen grains of *Lepidaploa* are mostly 45–50  $\mu\text{m}$  in diameter, only slightly larger on the average than those of *Xiphochaeta*. The elongate raphids in the wall of the achenes of *Xiphochaeta* are like those seen in the present study in *Lepidaploa* and its more specialized relatives, *Chrysolaela* H. Robinson, *Cyrtocymura* H. Robinson, *Echinocoryne* H. Robinson, *Eirmocephala* H. Robinson, and *Mattfeldanthus* H. Robinson & King. These raphids differ from the short form seen in two other *Lepidaploa* relatives, *Aynia* H. Robinson and *Lessingianthus* H. Robinson, and most other neotropical Vernoniaceae. No raphids have been observed in one other *Lepidaploa* relative, *Stenocephalum* Schultz-Bip.

*Xiphochaeta* is kept separate from *Lepidaploa*, which it most closely resembles, by the thickened pappus segments, by the short spurs on the anther thecae that are much shorter than the collars, and by the total lack of a sclerified carpodium. The carpodium of *Lepidaploa* is usually a well-developed turbinate structure covered with sclerified cells. The anther appendage of *Lepidaploa* is larger than that of *Xiphochaeta*, and usually lacks glands, but glands have now been seen in some plants of two species, a specimen determined as *L. helophila* (Mart. ex DC.) H. Robinson from Brazil and many Central American specimens of *L. canescens* (H.B.K.) H. Robinson.

Two of the distinctive features of *Xiphochaeta* involve reduction of parts, the unsclerified carpodium, and the reduced size of the anther thecae. Similar reduction of anther thecae, with collars longer than the spurs, is seen in members of the Vernoniaceae subtribe Elephantopinae, which are not closely related.

The genus contains a single known species occurring in the Guianas, the Orinoco basin, and the northern Amazon basin.

### ***Xiphochaeta aquatica* Poeppig in Poeppig & Endlicher**

syn. *Stilpnopappus viridis* Benth. ex Baker

*Stilpnopappus aquaticus* (Poepp. & Endl.) Dillon, Fieldiana, Bot. n.s. 11: 4. 1982.

#### ACKNOWLEDGMENTS

The SEM photographs were made mostly by Susann Braden using a Cambridge 250 Mk2 and a Hitachi S-570. Prints were prepared mostly by Sherry Pittam of the Department of Botany,

Smithsonian Institution. John Pruski of the New York Botanical Garden is thanked for information of the genus *Xiphochaeta*. This is publication #6 of the Biological Diversity of the Guianas Program, Smithsonian Institution.

## LITERATURE CITED

- BAKER, J. B. 1873. Compositae. I. Vernoniaceae. *In*: C. F. P. Martius, Ed., *Flora Brasiliensis* 6(2): 1–180.
- BENTHAM, G. AND J. D. HOOKER. 1873. Tribus I. Vernoniaceae. *Genera Plantarum* 2(1): 223–238.
- FUNK, V. A. 1991. The Compositae of the Guianas, I: Heliantheae (Heliantheae, Tageteae, Coreopsidae). *Rhodora* 93: 256–267.
- JEFFREY, C. 1988. The Vernoniaceae in east tropical Africa. *Kew Bull.* 43: 195–277.
- JONES, S. B. 1979. Chromosome numbers of Vernoniaceae (Compositae). *Bull. Torrey Bot. Club* 106: 79–84.
- . 1981. Synoptic classification and pollen morphology of *Vernonia* (Compositae: Vernoniaceae) in the Old World. *Rhodora* 83: 59–75.
- KEELEY, S. C. AND S. B. JONES. 1977. Taxonomic implications of external pollen morphology to *Vernonia* (Compositae) in the West Indies. *Amer. J. Bot.* 64: 576–584.
- KINGHAM, D. L. 1976. A study of the pollen morphology of tropical African and certain other Vernoniaceae (Compositae). *Kew Bull.* 31: 9–26.
- ROBINSON, H. 1987. Studies in the *Lepidaploa* complex (Vernoniaceae: Asteraceae). III. Two new genera, *Cyrtocymura* and *Eirmocephala*. *Proc. Biol. Soc. Wash.* 100: 844–855.
- . 1988. A new combination for *Vernonia libertadensis* S. B. Jones, with notes and descriptions of additional Andean species of *Baccharis*. *Phytologia* 65: 34–46.
- . 1990a. Six new combinations in *Baccharoides* Moench and *Cyanthillium* Blume (Vernoniaceae: Asteraceae). *Proc. Biol. Soc. Wash.* 103: 248–253.
- . 1990b. Studies in the *Lepidaploa* complex (Vernoniaceae: Asteraceae) VII. The genus *Lepidaploa*. *Proc. Biol. Soc. Wash.* 103: 464–498.
- . 1992. A new genus *Vernonanthura* (Vernoniaceae, Asteraceae). *Phytologia* 73(2): 65–76.
- STEETZ, J. 1864. *Crystallopollen and Ambassa*. *In*: W. C. H. Peters, Ed., *Naturwissenschaftliche Reise nach Mossambique auf Befehl seiner Majestät des Königs Friedrich Wilhelm IV. Part 6, Botanik.* 2: 363–364, pl. 48.
- STIX, E. 1960. Pollenmorphologische untersuchungen an Compositen. *Grana Palynol.* 2: 41–104, pl. 1–21.

DEPARTMENT OF BOTANY  
NHB - 166  
SMITHSONIAN INSTITUTION  
WASHINGTON, DC 20560